BEHAVIORAL INTERACTIONS AMONG FORMICID SPECIES IN THE ANT MOSAIC OF AN ORGANIC PEAR ORCHARD

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Abstract. —Structure of the ant mosaic of an organic pear orchard was studied. Based on behavior, colony dispersion, and colony size species inhabiting the pear orchard were categorized as follows: *Leptothorax muscorum* (Nylander), *Tapinoma sessile* (Say), and *Myrmica incompleta* Provancher were submissive species; *Lasius pallitarsis* (Provancher) were encounterers; the top level of the competitive hierarchy in the orchard was occupied by *Formica neoclara* Emery, a polygynous species, which has formed high density nests throughout the orchard. *Camponotus modoc* Wheller could not be categorized. Structure of the ant mosaic was very stable. Field surveys and pitfall traps showed that foraging territories of the ant species did not change over four years. There was considerable overlap in the spatial territories of the ant species. All six species foraged in pear trees and collected psylla honeydew, and all but *C. modoc* also were predators of pear psylla. However, they differed in their reliance on these food sources. Niches of each species were further differentiated by interspecific aggression and temporal mechanisms, especially ambient temperature and circadian cycles of behavior, which facilitated the coexistence of dominant and subdominant species.

Key Words. —Insecta, Formicidae, population structure, competition, ant interaction

In permanent habitats, such as forests and orchards, ants form a three-dimensional patchwork of nonoverlapping, foraging territories referred to as an ant mosaic. The distribution of each ant species within the mosaic is delineated by the availability of nesting material, nesting site preference, vegetation, abiotic requirements, availability of preferred food sources, and the intensity of intercolonial aggression (Savolainen & Vepsalainen 1988, Vepsalainen & Pisarski 1982, Jackson 1984, Leston 1973, Majer 1972).

Each mosaic is considered stable and able to withstand minor perturbations due to the elasticity of its components. However, major ecological changes will alter the structure of the mosaic. Disturbances associated with agroecosystems are examples of major changes that affect the ant mosaic. Common cultivation practices and the extensive use of pesticides simplify and destabilize the mosaic, often preventing beneficial ants from becoming permanently established (Altieri & Schmidt 1984, Leston 1973). For this reason, predation by ants in short term crops is insignificant unless the crop is grown next to a permanent habitat (Risch & Carroll 1982). In long term crops, such as in orchards, pesticide applications are almost entirely responsible for the breakdown of the ant mosaic. If the ant mosaic can be stabilized in an orchard, predatory ants can significantly contribute to the control of arthropod pests. Integrated pest management programs, incorporating modified spray schedules designed to conserve ant populations, have resulted in successful control of insect pests on cocoa and coffee plantations (Majer 1972, Leston 1973). Ants also contribute to the management of lepidopteran pests in coconuts (Way & Cammell 1989).

temperature readings of the soil (using a 15 cm probe), canopy, and ant trails were recorded with a telethermometer.

Pitfall traps were used in 1987–1989 to monitor ground activity of ants. Traps were constructed from 12 oz plastic cups. Approximately 20 ml of diluted anti-freeze (1:5 antifreeze : water) were poured into the cups, which were then buried up to their rim in the orchard. Pitfalls were collected after 24 h, and the contents examined under a dissecting microscope in the laboratory. Ants in the traps were counted and identified to species. Pitfall traps were rotated throughout the study area with 40–60 traps placed during each 24 h period. In three years 865 traps were examined.

Laboratory studies of inter- and intraspecific trail following behavior were carried out in the following manner. Two colonies of each ant species found in the orchard, except *L. muscorum*, were maintained in the laboratory. One colony of each species pair was given unrestricted access to food (honey and dead insects), which was removed 24 hours prior to testing. In the second colony, ants could obtain food only by climbing to the end of balsa wood sticks (5 × 10 × 20 mm long) inserted into the nesting material (approximately 45 degrees). In this way, foraging trails, established on the sticks, could be freely moved between colonies. A balsa stick was taken from a colony using a pair of forceps and, using caution to avoid agitating the ants, placed into a colony without sticks. The elapsed times were recorded, from the time of placement of the stick, until an ant located the food and a new foraging trail was established. Behavior of the ants in response to the trail (stick) was also observed. All possible intra- and interspecific combinations (25) were tested and replicated five times. Combinations were carried out in a random order with a new stick used for each test. Observations of *C. modoc*, a nocturnal forager, were carried out in simulated night conditions by using red lights.

Results and Discussion

Structure of the pear orchard ant mosaic was very stable. During the four years of this study field surveys and pitfall traps showed that foraging territories of the six ant species did not change. Even removal of a large portion of the mature trees had little effect on the mosaic, possibly because sprouting pear tree stumps proved to be a suitable replacement for lost trees. There was considerable overlap in spatial territories of ant species (Fig. 1). All six species were found foraging in pear trees and utilizing pear psylla honeydew as a food source and all, except *C. modoc*, also were predators of pear psylla.

However, ants differed in their reliance on pear psylla as a food source. *Formica neoclara* preyed almost exclusively on pear psylla (Paulson 1990) and collected large amounts of honeydew. Based on foraging intensity observed in the field, pear psylla honeydew was also an important food source for *L. pallitarsis,* but pear psylla (including honeydew) comprised only a small part of the diets of the other four species. Niches of each species within the orchard were further differentiated as the result of interspecific aggression and temporal mechanisms, especially ambient temperature and circadian cycles of behavior, which facilitated the coexistence of dominant and subdominant species (see below).

Nest sites of *F. neoclara, T. sessile, L. muscorum,* and *M. incompleta* also were spatially and temporally stable; nest locations (Fig. 2) of these species did not

In Washington, there are several key pests that affect orchard grown commodities, yet the beneficial role of ants in orchard systems has not been elucidated. One of the most damaging orchard pests is the pear psylla, *Cacopsylla pyricola* (Foerster). Heavy infestations can reduce yields by competing for available nutrients. Fruit production and value can be further reduced by the presence of honeydew, produced by the psyllids, which damages foliage and causes cosmetic russets on fruits, thereby decreasing their commercial value.

Presently, control of pear psylla is attained through the extensive use of pesticides. Chemical methods are not entirely successful, however. Spray programs fail when pesticide resistance develops in psylla populations. Damaging psylla population levels also may occur when pesticide use is discontinued prior to harvest. Ants can be valuable additions to a pear psylla management program. They remove substantial quantities of honeydew and are effective predators of pear psylla (Paulson 1990).

To effectively utilize ants in an integrated psylla control program, it is necessary to understand the structure of the ant community within a pear orchard. This study describes intra- and interspecific interactions within the ant community and the mediating effect of abiotic factors upon these interactions to form the ant mosaic.

MATERIALS AND METHODS

Field and laboratory studies elucidated the structure of the ant mosaic and the factors contributing to its formation and maintenance. Field studies were carried out from May–August during 1985–1989 in an organically managed orchard located near Peshastin, Washington. The study plot was initially 2 ha (approximately one-half of the orchard) of Bartlett pears (6 m × 6 m spacing), which was reduced to 1.5 ha in 1988 when most of the orchard was converted to pasture. Pear tree stumps, not removed from the pasture, sprouted. Therefore, after 1988, the study area was approximately 1.5 ha of mature pear trees and 0.5 ha of pasture/ pear shrubs. Ground cover, predominantly grasses, was kept short by regular mowing. Irrigation was applied with undertree sprinkler heads rotated through the orchard on a weekly basis. The orchard had not been treated with pesticides for at least 10 years. Six species of ants inhabited the orchard: *Formica neoclara* Emery, *Camponotus modoc* Wheeler, *Leptothorax muscorum* (Nylander), *Lasius pallitarsis* (Provancher), *Myrmica incompleta* (Provancher), and *Tapinoma sessile* (Say).

The structure of the ant mosaic was studied by direct observation of spatial and temporal changes in foraging behavior of each ant species, and by placing pitfall traps throughout the orchard. From May to September each year, observations were made at least once each week during the following time periods: 2400–0800, 0800–1200, 1200–1600, 1600–2000, and 2000–2400 hours. During each observation period every tree in the study plot was carefully examined to determine: the presence or absence of ants, the species observed, the relative abundance, and the distribution of each species in the tree, and inter/intraspecific interactions such as aggression, recruitment, and trail following. Locations of ant nests in the orchard were recorded. Several nests of each species were examined to determine colony size and nest structure. Care was taken to avoid destroying the nests. Colony size was extrapolated from partial counts of individuals. Hourly

A.

Foraging
Territory

Camponotus modoc
Tapinoma sessile
Leptothorax muscorum
Myrmica incompleta
Lasius pallitarsis
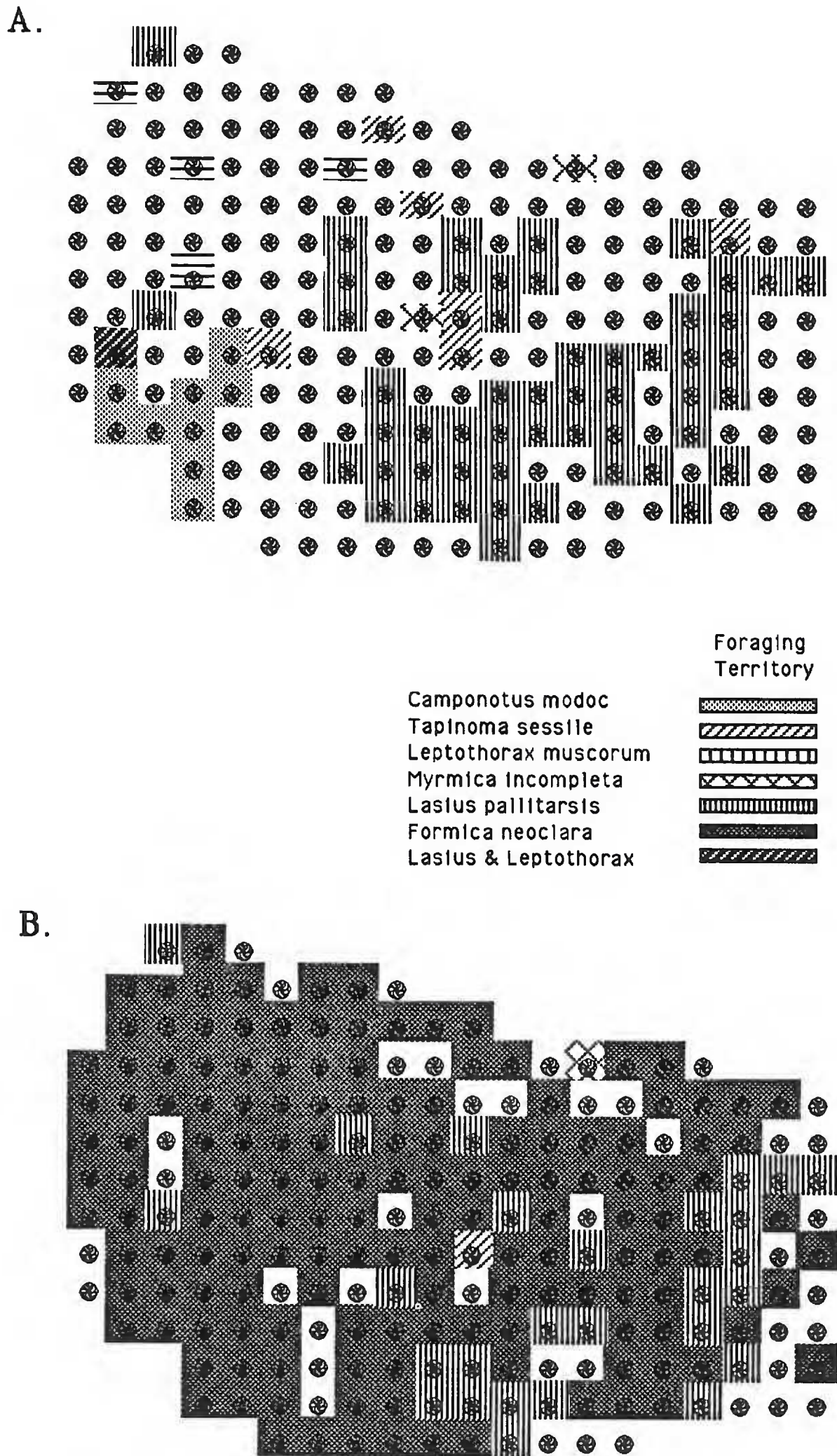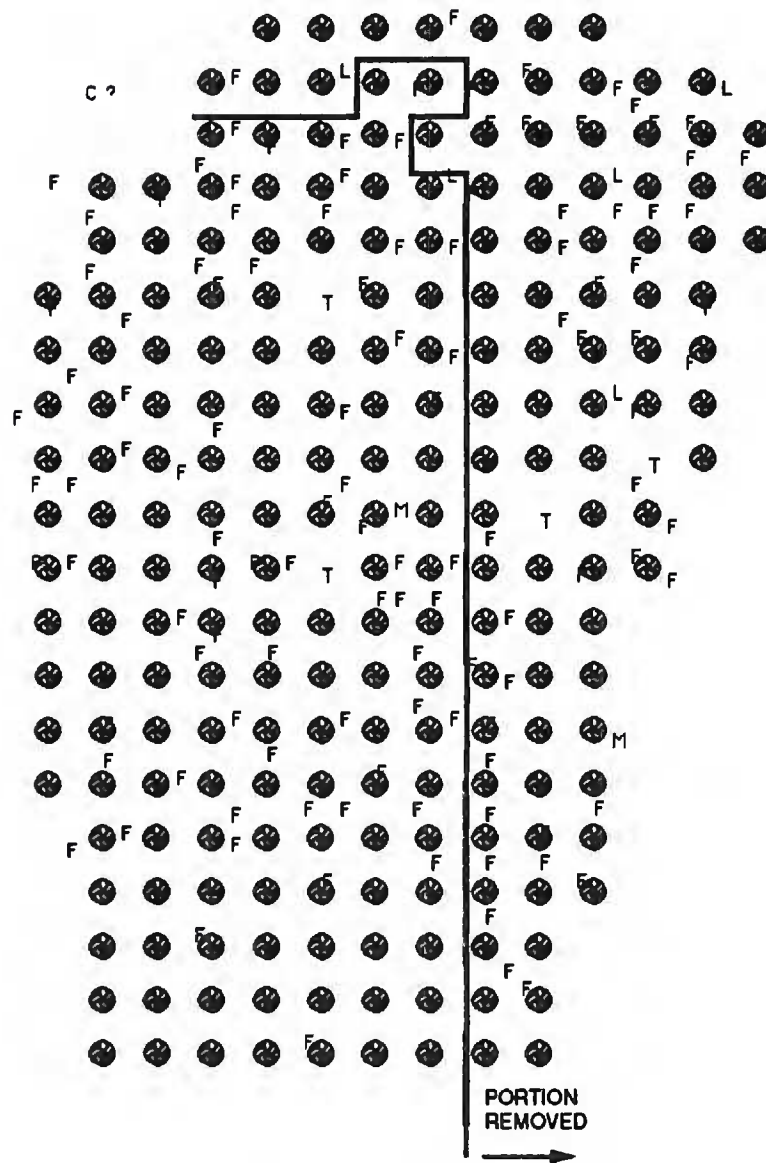Formica neoclara
Lasius & Leptothorax

B.

Figure 1.   Foraging territories (A, B) in the ant mosaic of an organic pear orchard in Peshastin, Washington. Individual trees are represented by circular symbols.

Nest

c	Camponotus modoc
T	Tapinoma sessile
L	Leptothorax muscorum
M	Myrmica incompleta
F	Formica neoclara

Figure 2. Nest sites in the ant mosaic of an organic pear orchard in Peshastin, Washington. Individual trees are represented by circular symbols.

change during this study. Of these species, *F. neoclara* had the greatest number of nests, 122, in the orchard. Only two nests of *M. incompleta,* four nests of *T. sessile,* and five nests of *L. muscorum* were found in the orchard. The nests of *Lasius pallitarsis,* a polygynous species, were difficult to locate and enumerate because the nests were cryptic and diffuse; the difficulty in discriminating nests may indicate the presence of a unicolonial nest assemblage. However, this possibility was not examined in this study. Due to the stability of the foraging areas of *L. pallitarsis,* it is reasonable to assume that its nest sites were also relatively stable. *Camponotus modoc* nests were never located.

Interspecific aggression was most responsible for the structure of the pear orchard ant mosaic. Vepsalainen & Pisarski (1982) divided the competitive hierarchy of ants into three levels. The bottom level, "submissives," defend only their nests. The intermediate level, "encounterers," also defend their food source. The

top level species, "territorials," additionally defend their foraging territories. Forager density (colony size) is positively correlated to competitive dominance (Savolainen & Vepsalainen 1988). Based on their behavior and colony dispersion and size, the species inhabiting the pear orchard were categorized: *L. muscorum*, *T. sessile*, and *M. incompleta* were submissive species; *L. pallitarsis* were encounterers; and the territorial level of the competitive hierarchy in the orchard was occupied by *F. neoclara*, a polygynous species which had formed high density nests throughout the orchard. The role of *C. modoc* is discussed below.

Submissive Species. — Field surveys and pitfall traps indicated that *M. incompleta*, *T. sessile*, and *L. muscorum* all had stable nest sites and temporal stability in their foraging areas, but did not have long term stability in their foraging trails. Foraging trails of *L. muscorum* and *M. incompleta* were regularly encountered, but rarely persisted for more than 2 days (respectively, means ± SD: 1.81 ± 0.08 d, $n = 26$; 1.58 ± 0.76 d, $n = 31$). *Tapinoma sessile* trails were slightly more persistent (2.12 ± 1.17 d, $n = 17$). Usually it was impossible to determine why a trail was terminated; however, on four occasions, *F. neoclara* was implicted as a probable cause for trail abandonment by *M. incompleta*. In these incidences *M. incompleta* were initially observed tending aphids. The following day both *F. neoclara* and *M. incompleta* were seen with the aphids. The ants did not appear antagonistic. During observation periods on subsequent days only *F. neoclara* were present and the aphid population declined until the aphids were gone. *Myrmica incompleta*, a submissive species, appeared to have been driven from the food resource.

In trail tests both *M. incompleta* and *T. sessile* responded most intensely to conspecific trails (Fig. 3). *M. incompleta* workers followed conspecific trails immediately (range <1 sec to 1 min), the number of ants responding to the trail was too intense to quantify. *Tapinoma sessile* workers responded to trails about as quickly as *M. incompleta* (range, 5 sec to 1 min), but less intensely. Maximum trail movement was about eight ants per minute moving toward the food source. The intensity and rapidity of recruitment to the food resource suggests that submissive ants exhibit a type of consumptive (exploitative) competition. When a food resource is located additional foragers are quickly recruited to maximize utilization of the resource before it is lost. The field observations described previously support this theory. Fellers (1987) reported that congeneric submissive (Fellers' "subordinate") species in a Maryland woodlot were also exploitative competitors.

In theory, exploitative ants should not recruit to food resources that are already being utilized by other ant species, especially those higher in the competition hierarchy, because there would be very little reward for the submissive ants. This was observed in the trail tests, further evidence that submissive ants are exploitative competitors. *Myrmica incompleta* workers appeared to sense the trails of other ant species. Workers would stop at the trails and have increased antennal movement, but did not follow those trails to the food. Similarly, *T. sessile* appeared to sense all the trails with which it was presented during this study, but it followed only conspecific trails and those of *M. incompleta* (response time, 2–3.5 min), another submissive ant.

Although reported (Smith 1928) to be polygynous, *T. sessile* colonies in this study were monogynous, as were all submissive species studied here. Nests of

SOURCE OF TRAIL

High – Low

Trail readily followed.

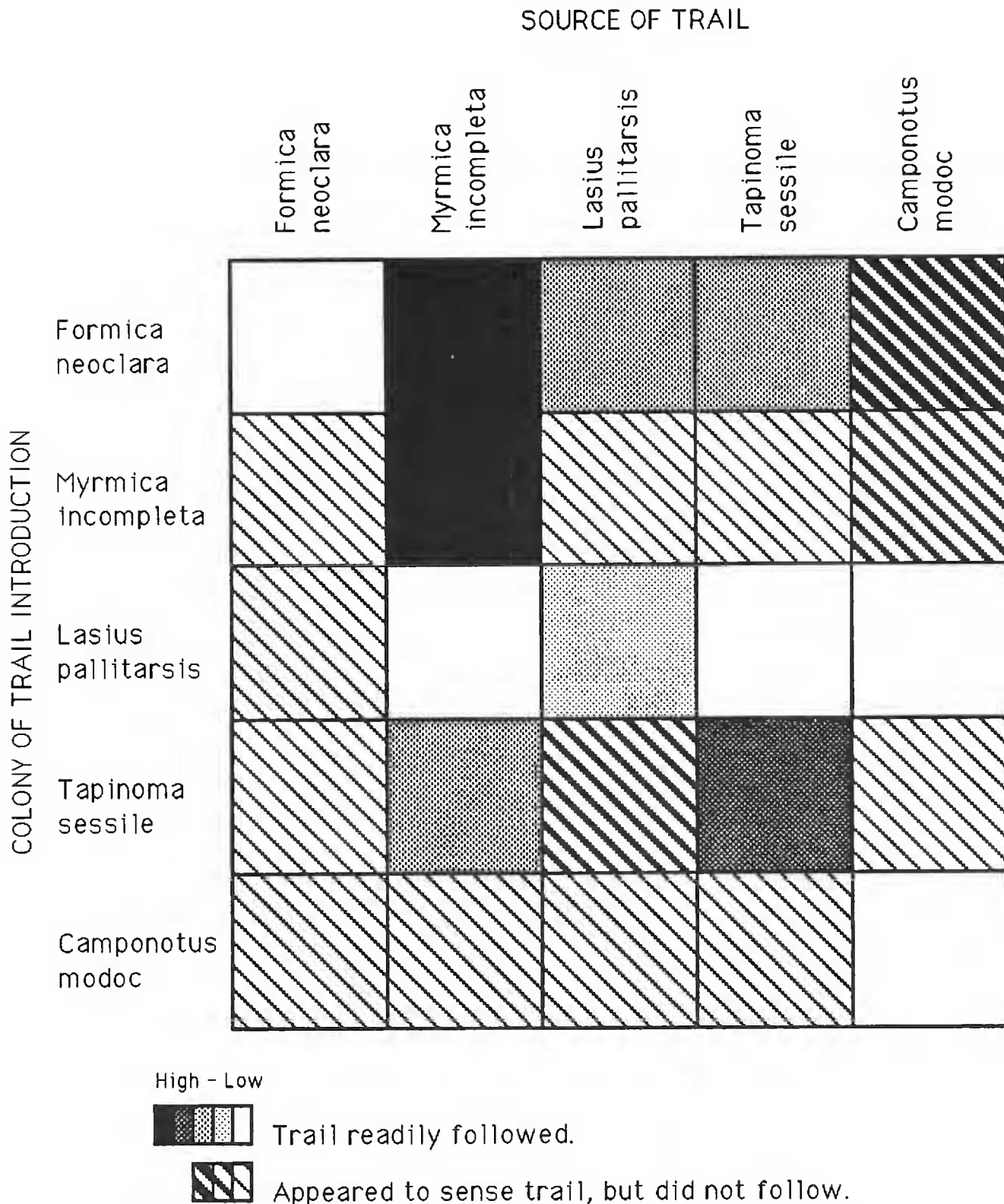Appeared to sense trail, but did not follow.

Figure 3. Matrix representing the relative intensity of ant worker response to foraging trails of five ant species.

submissive species were small. Average worker populations, based on estimates made during examinations of nests, were 1500 ($n = 2$, range, 500–2500) for *M. incompleta*, 5500 ($n = 3$, range, 2000–10,000) for *T. sessile,* and 2000 ($n = 3$, range, 1800–3000) for *L. muscorum.* Pitfall traps indicated that the submissive species had large foraging areas relative to colony size. All three species were generalist predators/scavengers. *Myrmica incompleta* was usually associated with aphids and was commonly found tending aphids infesting weeds in the orchard and the surrounding area.

Encounterer Species. —Lasius pallitarsis has many characteristics that indicate it is an encounter species. It is polygynous; nests were large and worker populations were estimated to be greater than 30,000. Nests and foraging territories had spatial
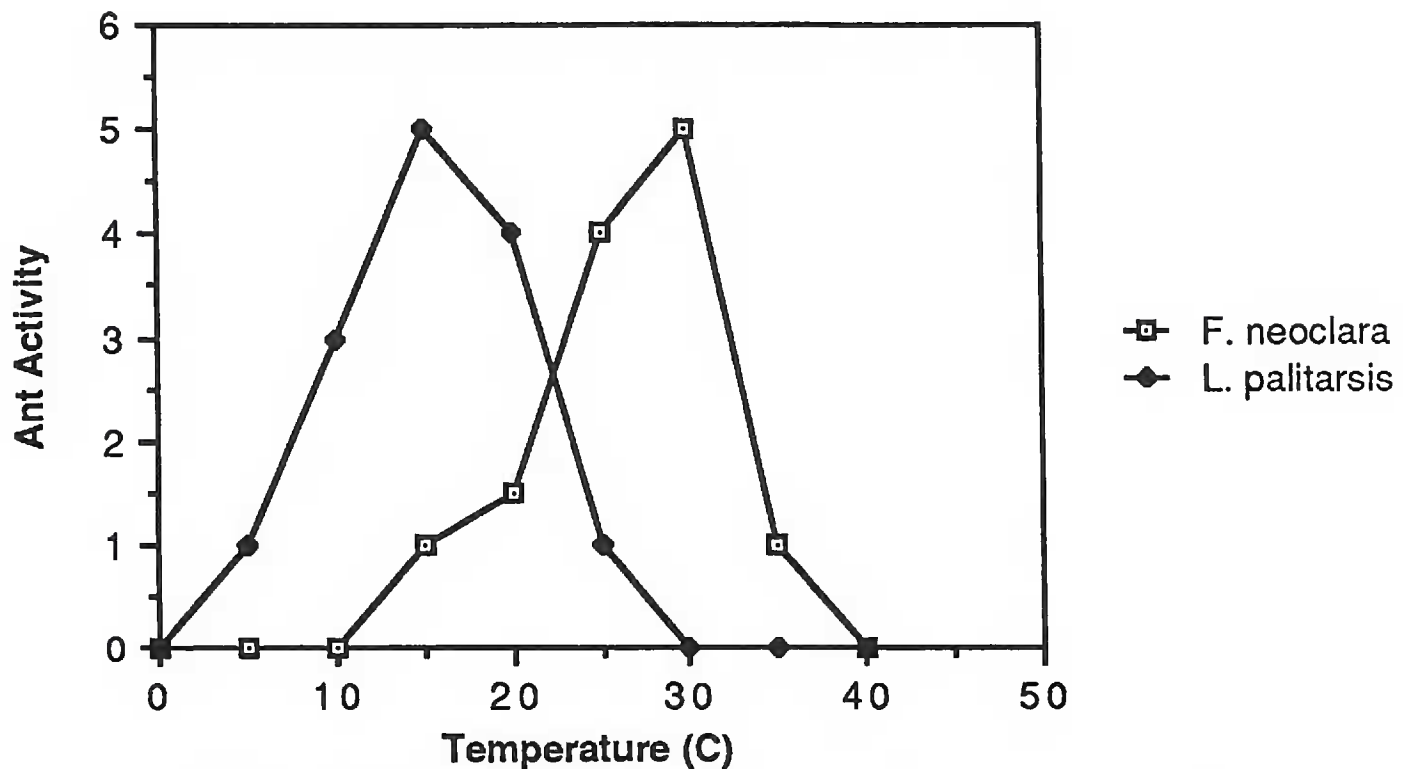
Figure 4.   Relative foraging activity of *Formica neoclara* and *Lasius pallitarsis* in a pear tree at different tree canopy temperatures.

and long term temporal stability. Foraging trails were maintained for long periods which was taken as evidence that trails were defended and maintained as long as the resource offered sufficient rewards. In trail studies, *L. pallitarsis* responded most intensely to conspecific trails, forming new trails in 3.5–5 min. *Lasius pallitarsis* also readily followed trails established by submissive species (*M. incompleta* in 4–10 min, *T. sessile* in 4–7 min) and by *C. modoc* (6–10 min) but would not follow trails of *F. neoclara*. Apparently *L. pallitarsis* would challenge all but the dominant ant species for access to a resource.

Lasius pallitarsis foraged heavily in the litter and also collected extensive amounts of pear psylla honeydew. During good foraging conditions, it was common to find trail flow on pear tree trunks in excess of 75 ants, engorged with psylla honeydew leaving the tree each minute. Due to the cryptic nature of *L. pallitarsis* nests and the difficulty of observing foraging efforts in the leaf litter, the importance of pear psylla honeydew in the diet of *L. pallitarsis* was not determined. Although *L. pallitarsis* and *F. neoclara* both utilized pear psylla as a major food resource, competition was diminished by thermal and temporal niche differentiation. *Lasius pallitarsis* foraging activity was related to tree canopy temperature. Peak foraging occurred between 10–18° C, which occurred between 0400–0600 h. Above 25° C, *L. pallitarsis* activity is negligible. This pattern of activity is the inverse of that of *F. neoclara,* which is rarely active below 15° C and most active at temperatures above 23° C (Fig. 4). Talbot (1942) found similar patterns of above ground activity in congeneric species of ants in a Michigan forest.

Territorial overlap of *L. pallitarsis* and *C. modoc* was slight (Fig. 1). Probably there is little overlap in the resource niches of these species, due to the extreme difference in worker size. Although both species will collect pear psylla honeydew, the resource is not utilized at the same time of day. *Camponotus modoc* is a nocturnal forager and *L. pallitarsis* is diurnal.

Camponotus modoc does not fit into the ant hierarchy as readily as the other species. It may be a species that only occasionally forages in the pear orchard and,

thus, is not truly part of the pear orchard ant mosaic. Foraging areas of *C. modoc* were spatially and temporally stable but were located on the edge of the orchard. A *C. modoc* nest was never located in or near the orchard. In addition, *C. modoc* did not regularly forage in the orchard and was found only in low numbers. All of these factors seem to indicate that *C. modoc* has a transient role in the orchard ant mosaic. In trail studies, *C. modoc* only responded to conspecific trails. Only *L. pallitarsis* would follow trails established by *C. modoc*. Upon encountering *C. modoc* trails, *F. neoclara* became agitated and had increased ortho- and klinokinesis, which were interpreted as an alarm response. Other *F. neoclara* workers were quickly recruited to this response.

The role of *C. modoc* cannot be readily defined. Although most evidence indicates that *C. modoc* is only a transient part of the ant mosaic, the response of *F. neoclara* to *C. modoc* trails may indicate another possible role. *Camponotus modoc* may be a potential co-dominant that is severely limited by the availability of nesting sites in the orchard.

Territorial Species.—*Formica neoclara* foraged almost exclusively in pear tree canopies collecting psylla honeydew and preying heavily on immature pear psylla (Paulson 1990). Foraging *F. neoclara* were found in about 70% of the pear trees. Tree surveys and pitfall trap collections indicated that virtually the entire orchard was *F. neoclara* territory. Nests and foraging areas were spatially and temporally stable. Although *F. neoclara* is polygynous, it did not form a unicolonial nest assemblage in the pear orchard. Foraging and nearest-neighbor studies of *F. neoclara* showed that nests are discrete colonies with high tolerance for conspecific ants (Paulson 1990).

In the field, trails were maintained as long as the resource was available. Trail-following studies showed that *F. neoclara* had a more rapid and stronger response to trails produced by other ant species than to those produced by conspecifics. By responding to trails in this manner, *F. neoclara* may strengthen its dominance by reducing intraspecific aggression while excluding submissive and encounterer ant species from shared resources. In the laboratory, *F. neoclara* quickly followed trails produced by *L. pallitarsis* (2.5–5 min), *M. incompleta* (1 sec–1 min), and *T. sessile* (1–6 min), and established its own foraging trails (Fig. 3). *Formica neoclara* formed new trails in response to conspecific trails in about 5 min (range, 3–8.5 min). As mentioned previously, *C. modoc* trails were not followed by *F. neoclara* and elicited an alarm response from this ant.

In summary, the structure of the pear orchard ant mosaic was very stable. Niche differentiation of each species within the orchard appeared to be predominately the result of interspecific aggression and temporal mechanisms, especially ambient temperature and circadian cycles of behavior, which facilitated the coexistence of dominant and subdominant species.

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